

COMPETITION AND NICHE REQUIREMENTS OF *COREOPSIS TINCTORIA*:
A WIDESPREAD BUT LOCAL HIGH DENSITY ANNUAL ASTERACEAE

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ABSTRACT

Coreopsis tinctoria (coreopsis, calliopsis, plains coreopsis, or golden wave) is an annual herbaceous Asteraceae with a broad geographic distribution mostly in the central and western United States. It co-occurs with *Bouteloua curtipendula* (sideoats grama) or other native C₄ grasses. When grown together, *C. tinctoria* response variables decreased significantly in the presence of *B. curtipendula* aboveground, belowground, and total dry mass. The response variables included mean plant height, number of flower buds per plant, flowers per plant, as well as aboveground, belowground, and total dry mass. The presence of *B. curtipendula* belowground dry mass caused the greatest suppression of *C. tinctoria* belowground dry mass. When *B. curtipendula* tops were clipped to reduce grass aboveground dry mass (simulated herbivory), the percent survival of *C. tinctoria* plants increased from one percent in the no-clipping treatment to 18% in the neighbor removal treatment (100% clipped). *Coreopsis tinctoria* does not appear to be a good competitor in the presence of *B. curtipendula* and seems to be restricted to gaps or patches in disturbed grasslands where competition from perennial grass neighbors is reduced.

Key Words: Belowground competition, aboveground competition, simulated herbivory, C₄ grass, *Bouteloua curtipendula*, sideoats grama, vegetation gaps, dry mass.

The North American Prairies once covered approximately 3.63×10^6 km² of the North American Continent. Today only a small percent (~1%) of the original prairies remain with most being converted to pasture or cropland (Barbour et al. 1999). On a large scale these still intact grassland communities seem stable and relatively uniform, but on a small scale, they more closely resemble a mosaic of successions or miniature successions started by disturbances that create gaps or patches in the communities (see Begon et al. 2006; Smith and Smith 2012). Fire, burrowing animals, large or small grazers (resulting in trampling of vegetation or intense grazing), and drought are often sources of disturbance in grassland habitats (Begon et al. 2006). These disturbance gaps or patches appear to serve as a reset mechanism (Pickett and White 1985) to reopen these mature communities to early successional species. The patch dynamics theory of community structure (see Begon et al. 2006) suggests that patches created by disturbance are initially recolonized by early successional species and then proceed in time toward a mature community. Vegetation gaps vary in shape, size, degree of vegetation removal (intensity), timing (recurring or uncommon), and spatial arrangement (McEvoy et al. 1993). Individual patches or gaps, created at different times, differ in their composition of early and late successional species. Thus, these disturbance patches or gaps should be viewed both temporally and spatially.

Establishment of early successional species increases with reduced competition (Cohn et al.

1989; Cahill and Casper 2002; Mazia et al. 2013), increased soil surface light levels, and soil resources (Bush and Van Auken 1986; Van Auken and Lohstroh 1990; Bush and Van Auken 2010). These characteristics are found in disturbances, clearings, openings, or gaps. Many annuals are opportunistic, early successional species that colonize grassland gaps created by disturbances (Begon et al. 2006). As time passes, other species, usually mid-successional or late-successional species, establish in these gaps or patches. These later species have different characteristics and requirements compared to the early successional species. With the change in species composition, from early to mid or late, the community characteristics would also change. Late successional communities do not have the highly repetitive disturbance characteristics of early communities (Bond 2008; Chaneton et al. 2012; Mazia et al. 2013).

Important factors in determining the success of seed or plant invasion into grassland communities are: (1) seed or propagule arrival or pressure, (2) community type and characteristics of the community being invaded or encroached, (3) the disturbance regime including type, size and frequency, and (4) biotic interactions (Bond 2008; Chaneton et al. 2012; Mazia et al. 2013). To be successful, early species or gap species usually have to produce large numbers of easily dispersed seeds. Once these seeds disperse into the grassland community they either germinate and establish immediately in newly created gaps or become part of the seed bank, surviving in the soil until a disturbance occurs (Baskin and

Baskin 2001). Once a seed has reached a site and germinated, intra- and interspecific competition are major factors determining establishment and future success (Mazía et al. 2013). Competition (a negative biotic effect) has been shown to cause major effects on plant growth, reproduction, and survival within natural communities and is often cited as a major factor in determining community composition and structure (Harper 1977; Connell 1983; Schoener 1983; Grace and Tilman 1990; Grelhier et al. 2012). Other factors have also been shown to influence community composition and structure, but which factor or factors are more important is undetermined (Callaway 1995; Bertness and Leonard 1997; Callaway and Walker 1997; Van Auken and Bush 1997; Wilson and Nisbet 1997; Pearson et al. 2011; Busch et al. 2012).

Competition's role in determining a species' distribution and community structure has been frequently examined. For example, the distribution of *Heterostipa neomexicana* (Thurb. ex J. M. Coult.) Barkworth, New Mexico feathergrass (= *Stipa neomexicana* [Thurb ex J. M. Coult.] Scribn.) was limited by competition from neighboring grasses that restricted it to less favorable grassland microhabitats (Gurevitch 1986). *Nassella leucotricha* (Trin. & Rupr.) R. W. Pohl (= *Stipa leucotricha* Trin. & Rupr., Texas wintergrass) a C₃ grass, was a better competitor than the co-occurring C₄ perennial grass, *Schizachyrium scoparium* (Michx.) Nash (little bluestem), at high light and nitrogen levels (White and Van Auken 1996). At low light and nitrogen levels competition was equal. However, *Schizachyrium scoparium* is probably a better competitor than *Nassella leucotricha* only at high temperatures. With other C₄ species, *Schizachyrium scoparium* appears to be an equal or better competitor in low nutrient soils (Bush and Van Auken 2010). Consequently, a combination of abiotic and biotic factors appears to determine species distributions. Density of *Coreopsis lanceolata* L., a herbaceous perennial, was negatively correlated with density of other species (Folgate and Scheiner 1992). Plants grew, survived, and reproduced better in areas where competitors were removed, especially if nutrients were added.

Species that appear to be poor competitors may be able to avoid competition by completing their life cycle before or after a competitor or by growing in areas where competition is reduced or absent (Eddy 2013). Many herbaceous C₃ species grow and complete their life cycle early in the growing season before C₄ plants start their growth. Poor competitors, including many annuals, grow in gaps or patches where their competitors, C₃ or C₄ perennial grasses, are not present or cannot complete their life cycle (Van Auken 2000; Cahill and Casper 2002).

Coreopsis tinctoria Nutt. is an annual herbaceous Asteraceae found throughout North Amer-

ican Prairies in the U.S., southern Canada, and northern México (Strother 2006). In some local areas density is high, but reasons for this are not clear and in many areas its density is very low (Correll and Johnston 1979). Grassland disturbance gaps appear to be areas where *C. tinctoria* is able to establish, grow, and complete its life cycle.

The purposes of the experiments reported here were to examine factors responsible for the growth and success of *C. tinctoria* in a native, southern, C₄ grassland. We hypothesized a reduction in the growth and dry mass production of *C. tinctoria* in the presence of a C₄ grass due to poor competitive abilities of *C. tinctoria*. We wanted to know if grass aboveground (shoot) or belowground (root) mass interference was equal or more important in suppressing *C. tinctoria* growth. We hypothesized that *C. tinctoria* growth characteristics would be reduced if the aboveground (shoot), belowground (root), or both aboveground and belowground dry mass of the grass was high. We expected the greatest reduction of *C. tinctoria* dry mass to be caused by belowground grass dry mass. We also hypothesized that survival of *C. tinctoria* seedlings in the field increase as grass dry mass decreases due to simulated herbivory.

METHODS

Field interspecific competition experiment. A field interspecific competition experiment between *C. tinctoria* (target) and *Bouteloua curtipendula* (Michx.) Torr. (matrix) was conducted to examine competition between the two species including potential differences among aboveground (shoot) and belowground (root) competition or a combination of both shoot and root competition. The experiment was started in April 1997 and was harvested 51–52 d later. The study was conducted at a field site on the University of Texas at San Antonio campus (98°37'47.93"W, 29°34'56.88"N). The soil in the experimental plot was a low nutrient, Patrick Series Mollisol, classified as a clayey over sandy, carbonatic-thermic, typic calciustoll (Taylor et al. 1966). The field site was dominated by *B. curtipendula* with *Cirsium texanum* Buckley and *Helianthus annuus* L. present as low-density species. The site was enclosed by a 1.8 m high chain-link fence to prevent large animal herbivory. Tap water was used to maintain the soil at field capacity. Four competition treatments of the matrix species with 10 replicates each were established in 40, 1 m × 1 m plots at the study site, including no roots/no shoots (NR/NS), roots/no shoots (R/NS), no roots/shoots (NR/S), and roots/shoots (R/S) (Gerry and Wilson 1995; McPhee and Aarssen 2001).

The no roots/no shoots (NR/NS) treatment was established by removing root (belowground) and shoot (aboveground) competition of *B. curtipendula* (Van Auken and Bush 1997). Root competition was removed by means of a 20 cm root excluder (20 cm deep \times 10 cm diameter \times 3 mm thick plastic PVC pipe). The root excluders were hammered into the ground to the level of the soil surface at the center of each NR/NS or NR/S plot and all live surface vegetation within the root excluder was manually removed. Shoot competition was removed with a 1 m \times 1 m wire mesh (4 cm \times 4 cm grid size). The mesh was placed over existing vegetation in plots (predominately *B. curtipendula*) and secured with 15 cm iron spikes at each corner. A 10 cm diameter opening was cut in the center of the mesh over the root excluder. All vegetation outside the root excluder was pulled away from the root excluder and pushed under the mesh, leaving no upright shoots to shade the target *C. tinctoria* plant.

The roots/no shoots (R/NS) treatment was established by removing only shoot competition. To mark the treatment location, a root excluder (2 cm deep \times 10 cm diameter \times 3 mm thick plastic PVC pipe) was hammered into the ground to the level of the surface soil at the center of each R/NS plot. Shoot competition was then removed by means of shoot excluders as described above.

The no roots/shoots (NR/S) treatment was established by removing only root competition. A 20 cm root excluder was used as described above and no shoot excluder was used.

The roots/shoots (R/S) treatment was established by allowing both root and shoot competition. A 2 cm root excluder was used as described above with no shoot excluder.

Coreopsis tinctoria seedlings were started from seed in 4 \times 4 \times 4 cm Jiffypot® (70% sphagnum peat moss and 30% wood fiber, Kristiansand, Norway) in a fiberglass greenhouse on the University Campus about 250 m from the field site. Five seeds were placed in each pot and covered with approximately two mm of soil. Any seeds germinating in excess of one were removed. After two weeks the seedlings in their associated Jiffypot® were transplanted to the field plot and one was randomly placed into the center of each root excluder. Plots were watered daily or as needed (depending on weather conditions) over the course of the experiment to maintain the soil at field capacity. Since previous work at the study site was affected by the presence of rabbits, and rabbit droppings were visible, a wire mesh cage (10 cm diameter \times 30 cm height; 1 cm \times 1 cm grid size hardware cloth) was placed over all transplants to exclude rabbits and rodents (Van Auken and Bush 1997).

Upon harvesting after 51–52 d, height (cm), number of flower buds, and number of flowers were measured or counted and recorded for each *C. tinctoria* plant. Shoots were then clipped at the

soil surface and dried to a constant mass in a forced air oven at 75°C. Root excluders were removed from the soil and placed into a 167 L plastic trash barrel containing a mixture of 15 liters tap water and 400 ml of sodium hexametaphosphate ($[\text{NaPO}_3]_6$) to loosen the soil from the roots. After soaking in the mixture for 24 h, the root excluders were removed and soil was washed from the roots by rinsing with a gentle stream of tap water. Roots free of soil were blotted dry, wrapped in aluminum foil with holes for ventilation and dried to a constant mass in a forced air oven at 75°C. Roots were then ashed at 600°C for three hours (Böhm 1979) to determine the mass of any adhering soil particles and ash-free root dry mass was calculated.

Shoot, ash-free root, and total dry mass were measured per plant for *C. tinctoria*. All remaining vegetation (*B. curtipendula* and low-density species, including *Cirsium texanum* and *Helianthus annuus*) in each 1 m \times 1 m plot was clipped at the soil surface, stored in paper bags, and allowed to air dry to a constant mass in a fiberglass greenhouse. Shoot dry mass was weighed to determine per plot dry mass and then mean dry mass was calculated per treatment. *Bouteloua curtipendula* shoot dry mass per plot was analyzed with a one-way ANOVA with competition treatments (NR/NS, R/NS, NR/S, and R/S) as the independent variable (Sall et al. 2012). Significant differences were not detected ($P > 0.05$).

A multivariate one-way analysis of variance (MANOVA) was completed for all *C. tinctoria* measured parameters. When the MANOVA was significant (Pillai's Trace, $P < 0.05$), separate one-way ANOVAs were performed with treatment (NR/NS, R/NS, NR/S, and R/S) as the independent variable. If significant differences were detected among any of the response variables and the treatment variable, a Scheffé Multiple Comparison test was employed for pairwise comparisons among individual treatments. In addition, a Shapiro-Wilk test was used to test for normality and Levene's test was used to test for equal variance (Sall et al. 2012).

Field simulated neighbor herbivory experiment. *Coreopsis tinctoria* survival in an established grassland was also examined in a field experiment as a function of *B. curtipendula* shoot height. The experiment was conducted at the same field site described above and was started in September 1997 and harvested after 61 d. Three levels of grass height were established in three, 0.6 m \times 2.1 m (1.26 m²), study plots dominated by *B. curtipendula* with associated low-density species including *C. texanum* and *H. annuus*. Clipping or simulated herbivory of *B. curtipendula* shoot height was used as an alternative to density or biomass. Clipping has a negative overall effect on

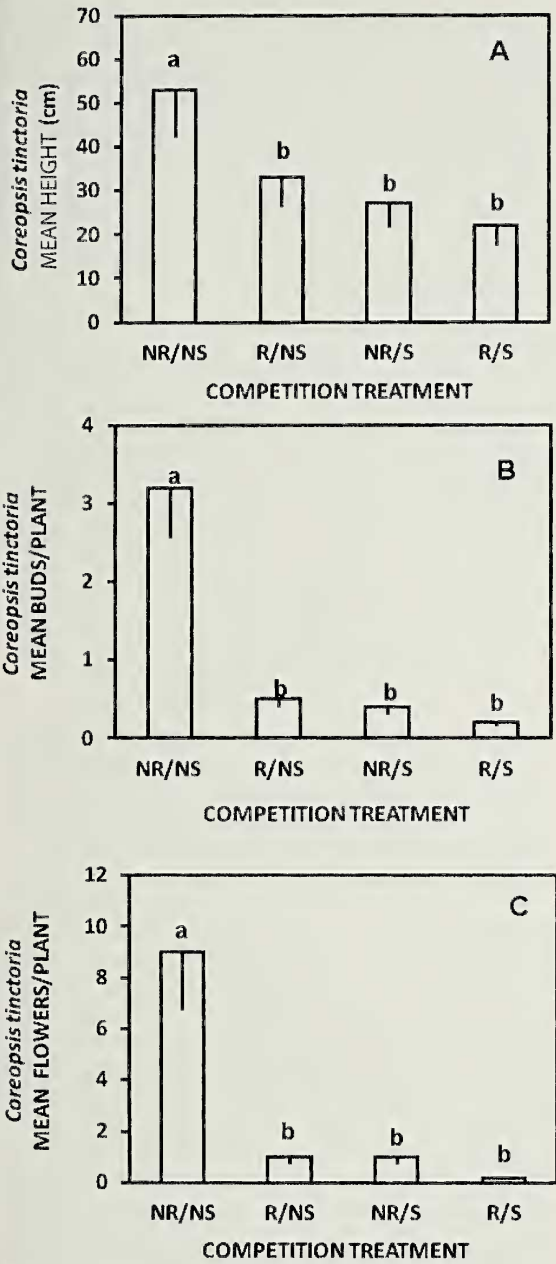


FIG. 1. Mean *Coreopsis tinctoria* height in cm (A), number of flower buds per plant (B), and the number of flowers per plant (C) as a function of competition treatment. Treatments were no roots/no shoots (NR/NS), roots/no shoots (R/NS), no roots/shoots (NR/S), and roots/shoots (R/S) with 10 replications each. There were significant differences in all response variables (MANOVA, Pillai's trace, $P = 0.0001$) and significant increases in all response variables in the absence of competition (NR/NS, one way ANOVAs, $P < 0.01$ for all). Different lower case letters indicate significant differences among treatments (Scheffé Multiple Comparison Test) and lines are -1 SD.

plant mass. Treatments were no herbivory (0% clipping), partial herbivory (clipping and removal of 50% of the normal grass height), and maximum herbivory or total grass height and biomass removal (100% clipping). *Bouteloua curtipendula* shoot biomass in the study plots was estimated by clipping all vegetation at the soil surface in five, $0.5\text{ m} \times 0.5\text{ m}$, quadrats adjacent to the study plots. Average shoot dry mass per quadrat was determined after drying to a constant mass in a forced air oven at 75°C . Mean (\pm SD) *B. curtipendula* aboveground biomass was $476 \pm 69\text{ g/m}^2$ in the no herbivory plots. *Coreopsis tinctoria* seedlings were started with excess seed in $4 \times 4 \times 4\text{ cm}$ Jiffypot® (70% sphagnum peat moss and 30% wood fiber, Kristiansand, Norway) in a fiberglass greenhouse as above. After two weeks seedlings were thinned to one plant per pot and transplanted into the field in their associated Jiffypot®. One hundred seedlings, five rows of 20 seedlings each, were planted 10 cm apart and 10 cm from the edge in each plot and marked to aid in locating the plants. Plots were watered daily or as needed (depending on weather conditions) over the course of the experiment to maintain soil field capacity. Every four days each plot was examined and seedling mortality was recorded.

Coreopsis tinctoria survival in the three herbivory treatments (0%, 50%, and 100% clipping) was compared using a two-tailed χ^2 test. Significant differences in *C. tinctoria* survival were found among the three herbivory treatments; therefore, three one-tailed χ^2 tests were completed to examine significant differences among individual treatments (Mendenhall and Beaver 1994).

RESULTS

Field interspecific competition experiment. Total competition (aboveground shoot and belowground root) and differences in aboveground and belowground competition were examined with *C. tinctoria* as the target species and *B. curtipendula* as the matrix or competitor species. Initial mean *B. curtipendula* aboveground (shoot) dry mass (\pm one SD) in the forty, $1\text{ m} \times 1\text{ m}$, study plots was $287.5 \pm 42.5\text{ g/m}^2$ with no significant differences among treatments (One-way ANOVA, $F = 1.61$, $P > 0.05$).

A MANOVA was used to do an overall comparison of all measured response variables in the field interspecific competition experiment. Pillai's trace was significant ($P < 0.0001$, Figs. 1 and 2) indicating that competition from *B. curtipendula* significantly affected *C. tinctoria* measured response variables. *Coreopsis tinctoria* mean height was significantly greater when plants were grown in the no competition treatment (NR/

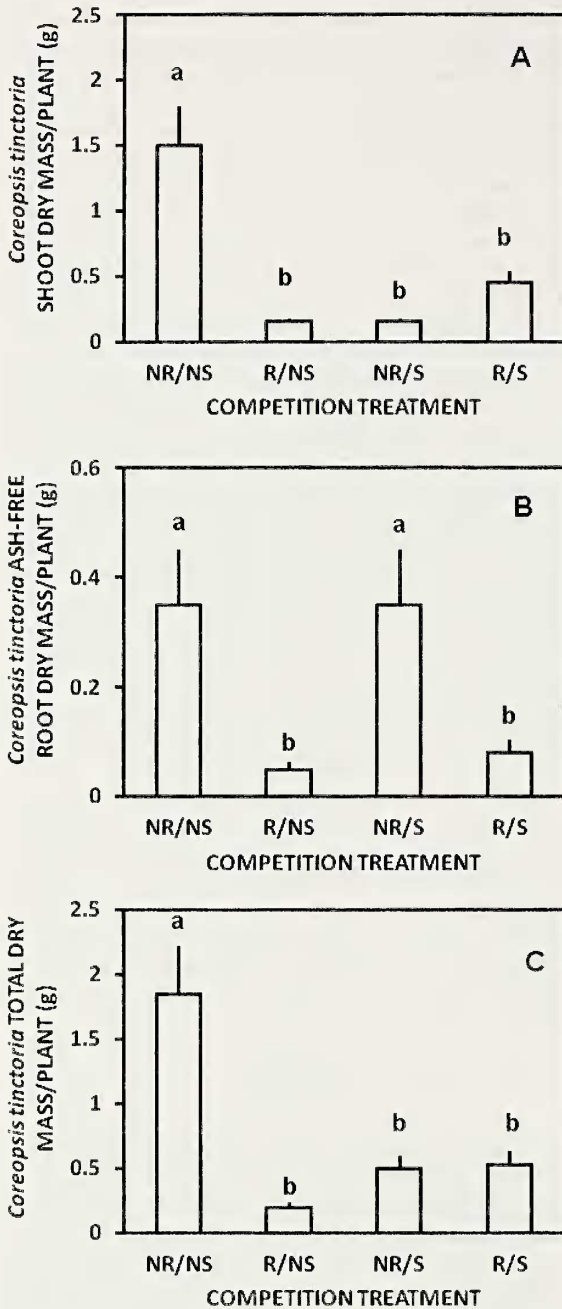


FIG. 2. Mean *Coreopsis tinctoria* aboveground dry mass (A), ash free root dry mass (B), and total dry mass per plant (C) as a function of competition treatment. Treatments were no roots/no shoots (NR/NS), roots/no shoots (R/NS), no roots/shoots (NR/S), and roots/shoots (R/S) with 10 replications each. There were significant differences in all response variables (MANOVA, Pillai's trace, $P = 0.0001$) and significant increases in all response variables in the absence competition (NR/NS, one way ANOVAs, $P < 0.001$ for all). For ash free root dry mass, when roots of the grass were removed (NR/NS or NR/S) there was an increase in *C. tinctoria* root dry mass. Different lower case letters indicate significant differences among treatments (Scheffé Multiple Comparison Test) and lines are +1 SD.

NS, Fig. 1A, one-way ANOVA; $F = 22.39$, $P < 0.0001$, Scheffé Multiple Comparison Test). Mean height of *C. tinctoria* decreased 40–58% from 53 cm in the no competition treatment to 22–32 cm with root or shoot competition, or when both root and shoot competition was present. Mean height was not significantly different among treatments with root or shoot competition or both roots and shoots present (R/NS, NR/S, or R/S, $P > 0.05$, Scheffé Multiple Comparison Test) (Fig. 1A).

The mean number of flower buds per plant was significantly greater when *C. tinctoria* plants were grown with no competition (Fig. 1B, one-way ANOVA; $F = 6.03$, $P < 0.01$, Scheffé Multiple Comparison Test). The mean number of flower buds per plant decreased 67–99%, from approximately three flower buds per plant in the no competition treatment to less than one flower bud per plant with root competition, shoot competition, or when both root and shoot competition was present. The mean number of flower buds per plant was not significantly different among treatments with root or shoot or both root and shoot competition present ($P > 0.05$, Scheffé Multiple Comparison Test). The mean number of flowers per plant was significantly greater when plants were grown in the no competition treatment (Fig. 1C, one-way ANOVA; $F = 7.12$, $P < 0.001$, Scheffé Multiple Comparison Test). The mean number of flowers per plant decreased 90–99% from approximately nine flowers per plant in the no competition treatment to less than one flower per plant with root competition, shoot competition, or when both root and shoot competition was present. The mean number of flowers per plant was not significantly different among treatments with root or shoot or both root and shoot competition present ($P > 0.05$, Scheffé Multiple Comparison Test).

Coreopsis tinctoria mean aboveground or shoot dry mass per plant was significantly greater when plants were grown in the no competition treatment (Fig. 2A, one-way ANOVA, $F = 73.49$, $P < 0.0001$, Scheffé Multiple Comparison Test). Mean shoot dry mass per plant decreased 74–90%, from 1.49 g in the no competition treatment, to 0.15–0.39 g when root competition, shoot competition, or when both root and shoot competition was present with no significant differences among them ($P > 0.05$, Scheffé Multiple Comparison Test). Significant differences in *C. tinctoria* mean belowground or ash-free root dry mass per plant were also detected. Mean ash-free root dry mass per plant was greatest in the no root, no shoot competition treatment (0.36 g) and least in the root only competition treatment (R/NS, 0.07 g) (Fig. 2B, one-way ANOVA; $F = 58.90$, $P < 0.0001$, Scheffé Multiple Comparison Test). Significant reductions in mean

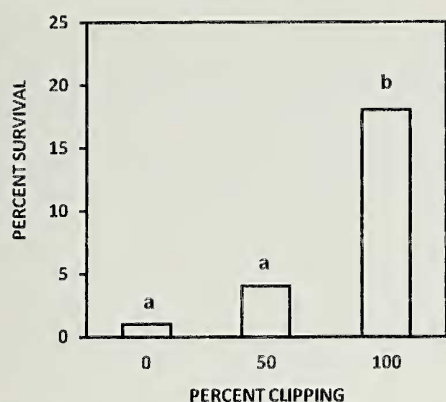


FIG. 3. Percent survival of *Coreopsis tinctoria* seedlings as a function of aboveground grass height reduction (clipping, 0%, 50%, 100%). Survival of *C. tinctoria* was significantly affected by clipping (two-tailed X^2 test, $X^2 = 19.75$, $df = 2$, $P < 0.01$). Survival was significantly greater in the 100% clipping treatment than the 50% treatment (one-tailed X^2 test, $X^2 = 7.53$, $df = 1$, $P < 0.01$) and 0% treatment (one-tailed X^2 test, $X^2 = 15.20$, $df = 1$, $P < 0.01$). Different lower case letters indicate significant differences between survival in the clipping treatments (one-tailed X^2 test).

ash-free root dry mass occurred when grass roots were present (R/NS and R/S) compared to the no root treatments (NR/NS and NR/S), but there were no differences between either of the two treatments with roots or those two treatments without roots ($P > 0.05$, Scheffé Multiple Comparison Test).

Results for mean total *C. tinctoria* dry mass per plant and mean shoot dry mass per plant were similar (Fig. 2C). Highest mean total dry mass was 1.85 g per plant in the NR/NS treatment. Total *C. tinctoria* dry mass per plant decreased significantly with the presence of root or shoot or both root and shoot total grass dry mass per plant (Fig. 2C, one-way ANOVA, $F = 58.89$, $P < 0.0001$). However, *C. tinctoria* total dry mass per plant was not significantly different among treatments with root or shoot or both root and shoot grass dry mass present ($P > 0.05$, Scheffé Multiple Comparison Test). Mean *C. tinctoria* total dry mass per plant was between 0.20 and 0.53 g when either grass roots or shoots or both were present, a reduction of 71–89%.

Field simulated neighbor herbivory experiment. *Coreopsis tinctoria* survival as a function of aboveground grass dry mass or competition in an established grassland was also examined. Mean (\pm one SD) *B. curtipendula* aboveground or shoot dry mass per quadrat in the study plots (estimated in five, 0.5 m \times 0.5 m, quadrats adjacent to the study plots) was 475.98 ± 58.67 g/m². Simulated herbivory or clipping significantly affected *C. tinctoria* seedling survival in the field (Fig. 3, two-tailed X^2 test, $X^2 = 19.75$, $df =$

2, $P < 0.01$). *Coreopsis tinctoria* survival was 1% at 0% grass clipping or no aboveground grass removal and was not significantly different than survival at 50% grass clipping which resulted in 4% *C. tinctoria* survival (one-tailed X^2 test, $X^2 = 2.66$, $df = 1$, $P > 0.05$). However, *C. tinctoria* survival at 100% grass clipping (zero grass aboveground dry mass) was significantly greater than at 50% clipping (one-tailed X^2 test, $X^2 = 7.53$, $df = 1$, $P < 0.01$) and 0% clipping (one-tailed X^2 test, $X^2 = 15.20$, $df = 1$, $P < 0.01$). Greatest survival after 61 d was 18% in the 100% simulated herbivory or grass clipping treatment (100% neighbor removal).

DISCUSSION

Plants compete for aboveground and belowground resources simultaneously and determining which resources are more important has been difficult to resolve (Harper 1977; Grime 1979; Wilson and Keddy 1986; Tilman 1988; Grace and Tilman 1990; Keddy 2001). Many experimental grassland studies have shown that aboveground and belowground competition reduces dry mass in most if not all associated species, but aboveground dry mass may be more important in reducing community diversity (Lamb et al. 2009). Light levels are reduced more than 50% under the grassland matrix shading neighbors and limiting germination or growth of many herbaceous species in grassland communities (Bush and Van Auken 1987; Collins et al. 1998; Haag et al. 2004). Belowground biomass in grassland habitats can be two to four times higher than aboveground biomass and as much as 80% is found in the top 25 cm of soil (Risser et al. 1981; Bush and Van Auken 1991; Cahill 2003).

As a result of the intense competition experienced in intact grasslands, species with poor competitive abilities are sometimes restricted to unproductive sites where competition is minimal (Cahill and Casper 2002). Grime (1977) suggested that a trade-off exists between a species competitive ability and its stress tolerance. Habitat specificity of *Coreopsis lanceolata* appears to be related to both its tolerance of low soil nutrients and poor competitive ability, supporting the theory of a trade-off (Grime 1977). With neighbors removed *C. lanceolata* was capable of growth and survival on both productive sites and stressful sites with reduced nutrient soils. Morphological traits, growth rates, survivorship, and reproduction of *C. lanceolata* were all reduced with competition (Folgate and Scheiner 1992) and it was restricted to vegetation gaps or non-productive habitats.

It appears that distribution of *Coreopsis tinctoria* is restricted to disturbed habitats or to early season growth as a result of the spatial and temporal competition it encounters in established

grasslands. In the field, *C. tinctoria* growth requirements or niche requirements probably limit it to large or small disturbances in grasslands communities, as was shown for *C. lanceolata* (Folgate and Scheiner 1992). After a disturbance such as grazing, fire, or a large scale, multi-year drought C_4 grasses are reduced (Barbour et al. 1999). Annuals with seeds in the seed bank, like *C. tinctoria*, exploit the lack of competition occurring until the C_4 grasses recover their former dominant community position. During the early growth period, soil nutrients from decomposition are higher and available for uptake by early season C_3 herbaceous annuals like *C. tinctoria*, while the C_4 grasses are still mostly dormant (McKinley and Blair 2008). *Coreopsis tinctoria* seems to be tolerant of lower temperatures than associated C_4 grasses and grows well both in cooler latitudes and early in the growing season (Cahill 2003), but not during the hot, dry, southwestern summers (Enquist 1987). *Coreopsis tinctoria* seems to be able to grow in a southern grassland matrix in the absence of gaps by establishing early in the growing season (Eddy 2013), before the C_4 grasses start their growth (Cahill 2003).

Results from field experiments presented here lead to the same conclusions, *C. tinctoria* is a poor competitor and only found in disturbed sites or in gaps, probably in the early southern growing season or after droughts (Figs. 1 and 2). When *C. tinctoria* was examined in plots that were clipped to simulate grass herbivory (Fig. 3), survival was greatest in plots with all aboveground grass removed. When *C. tinctoria* was grown with *B. curtipendula* in an experiment to examine the importance of aboveground, belowground, and total grass biomass, almost all of *C. tinctoria* response variables increased with almost all grass reduction treatments. Aboveground and total grass dry mass appeared to be equally detrimental to *C. tinctoria*'s response variables (Figs. 1 and 2). However, belowground dry mass of *B. curtipendula* in any combination reduced the belowground dry mass of *C. tinctoria*.

Species restricted to stressful, unproductive sites are not necessarily excluded under all conditions. With grassland disturbances such as grazing, mowing, fire, and extended drought, gaps are opened in the matrix and offer a mechanism of entry into productive established communities to species with reduced competitive abilities. Both aboveground and belowground competition from dominant matrix species is reduced in gaps or patches, making establishment and growth possible for poor competitors (Cahill and Casper 2002). Grazing and mowing have been shown to create aboveground and belowground gaps (Bush and Van Auken 1987; Collins et al. 1998; Haag et al. 2004), increasing surface

light levels by 100% and decreasing belowground biomass of dominant matrix species (Collins 1987; Van Auken and Bush 1989, 1990; Bush and Van Auken 1991; Collins et al. 1998; Cahill and Casper 2002). High species diversity in C_4 grasslands is characterized by large numbers of C_3 forbs. Seeds of many of these C_3 forbs remain dormant in the seed bank until either one or a combination of these disturbances open a gap in the grassland matrix that allows their germination and establishment (Collins et al. 1998). This mechanism of entry into established grasslands by utilizing gaps as sites of establishment is apparently also an important mechanism used by early successional species (Collins 1987; Van Auken and Bush 1989; Bush and Van Auken 1991, 1995; Bond 2008; Chaneton et al. 2012; Mazia et al. 2013).

Previous unpublished greenhouse studies with *Coreopsis tinctoria* (Elliott 1999) have shown that both aboveground and belowground grass dry mass reduce the dry mass of *C. tinctoria*, suggesting that grass competition or a lack of competition was important for the success of *C. tinctoria*. Mortality of *C. tinctoria* was approximately 70% in a northern C_3 grassland, with neighboring grass roots apparently inconsequential, but biomass of *C. tinctoria* was reduced by more than 80% in the presence of the grass roots (Cahill 2003), and effects of insect herbivory was mixed (Haag et al. 2004).

In addition to gaps, the timing of growth of two potentially competing species from the same habitat seems to be important in determining their local distribution and density (Eddy 2013). A C_4 grass like *B. curtipendula* has high water and nitrogen use efficiencies, high light and temperature requirements, and grows best late in the growing season, especially in hot southern grasslands (Fay et al. 2003; Weatherford and Myster 2011). A target C_3 woody plant (*Prosopis glandulosa* Torr.) grown in competition with *B. curtipendula* had 10–20 times more total dry mass when planted two months before the C_4 grass but was suppressed 99.9% if planted with the grass but two months after the grass was started (Bush and Van Auken 1991).

Coreopsis tinctoria density is low in the matrix of southwestern grasslands and possibly missed in cursory surveys, especially after the main C_4 grasses start their growth, and *C. tinctoria* has completed its life cycle (Correll and Johnston 1979). High densities of *C. tinctoria* have only been noted in relatively large displays, seemingly in large gaps or disturbances where the C_4 grasses are reduced or early in the growing season (Elliott and Van Auken, personal observation). Differential timing of growth, intense competition from associated species, inherent lack of competitive ability, and tolerance of low nutrient soils all result in local variability in density of *C. tinctoria* despite its widespread distribution.

CONCLUSIONS

In the field, *Coreopsis tinctoria* grows poorly or not at all with *B. curtipendula*, a perennial C₄ southern grass. *Coreopsis tinctoria* appears to be a species that requires large or small disturbances or gaps or it grows early in the growing season before the C₄ grasses become active at higher temperatures. When found in native communities, it seems to be a good indicator of disturbances. These disturbances are caused by man, herbivory, burrowing of small mammals, fire, or drought, or combinations of these factors.

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